

# THE GENUS *RYTIDOSPERMA* (POACEAE) IN THE UNITED STATES OF AMERICA

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## ABSTRACT

The genus *Rytidosperma* is a group of southern hemisphere grasses in the subfamily Danthonioideae. Several species have been introduced in forage trials into regions of the United States, of which 5 have become naturalized in California, Oregon and Hawai'i in grasslands and ruderal habitats. The species present in the USA are described and new chromosome counts are reported for *R. racemosum* and *R. richardsonii* from California, and *R. caespitosum* from New Zealand.

## RÉSUMÉ

Le genre *Rytidosperma* est un groupe de graminées de la sous-famille Danthonioideae de l'hémisphère sud. Plusieurs espèces ont été introduites dans des régions des États-Unis pour essais fourragères, dont 5 ont été naturalisées en Californie, Oregon et Hawaii dans les prairies et les habitats rudérales. Les espèces vivant aux États-Unis sont décrites et le nombre de chromosome est signalé pour *R. racemosum* et *R. richardsonii* en la Californie, et *R. caespitosum* en Nouvelle-Zélande.

## INTRODUCTION

Previously included in *Danthonia* sensu lato, *Rytidosperma* is genus of grasses in the subfamily Danthonioideae with about 45 species that are native to Australia, New Zealand, New Guinea, southern South America, and possibly India (Connor & Edgar 1979). Clayton and Renvoize (1986) distinguished *Rytidosperma* from *Danthonia*, but included the African species of *Karroochloa* and *Merxmulleria* in the former. A narrower generic circumscription of *Rytidosperma* was advocated by Linder & Verboom (1996), who recognized various generic segregates, but acknowledged that "there is an almost equally strong case for recognizing a single, large genus, *Rytidosperma*" (p. 607). According to their interpretation, all species treated here would be placed in *Austrodanthonia* H.P. Linder (Linder 1997, 2005). However, a clear and consistent separation of *Austrodanthonia* from *Rytidosperma* cannot be achieved using the morphological characteristics they provided (cf. Connor & Edgar 1979), and is not supported by the extensive DNA sequence analysis of Pirie et al. (2008). The detailed phylogenetic analysis of Danthonioideae genera by Linder et al. (2010) considers a somewhat intermediate circumscription of *Rytidosperma* approaching that of Clayton and Renvoize (1986) and including all the species treated here. These authors discuss in detail the merits and deficiencies of various options for delimiting *Rytidosperma* and other genera in the Danthonioideae.

Species of *Rytidosperma*, under the names *Danthonia pilosa* and *D. semiannularis*, were imported into New Zealand as seed harvested by mechanical field strippers from natural grasslands in Australia, and sown in seed mixes for grassland improvement (Zotov 1963). They were probably distributed elsewhere in the world for trials. Several species of *Rytidosperma* have been cultivated in research plots or forage trials in both the United States (Weintraub 1953) and Canada under names which are mostly incorrect and for which the original geographic source is obscure (see especially specimens listed under *R. penicillata* below).

Naturalization in the US appears to have occurred only in California, Oregon and Hawai'i (Whitney et al. 1939; Darbyshire & Connor 2003; Dean & al. 2008).

The genus *Rytidosperma* is distinguished from *Danthonia* sensu stricto primarily by the presence of transverse rows of hairs on the back of the lemma (Figs. 1–3). These hairs may be in discrete tufts or form more or less continuous lines. One row occurs towards the base just above the callus and the other towards the apex just below the awn sinus. Rows, especially the upper, may be reduced to tufts only at the margins. Other hairs may or may not be scattered across the back of the lemma between the rows. In some species the lemma back indumentum may be lacking altogether, while in other species the lemma back is more or less evenly covered by hairs with no distinct trace of the two rows of tufts. Ensheathed spikelets, cleistogenes, were reported by Chase (1918) in the leaf axils of many species of *Danthonia* (including "*D. semiannularis*"), but these are absent from *Rytidosperma* (Vickery 1956; Connor & Edgar 1979). Florets of the exerted inflorescences may be either chasmogamous or cleistogamous (Edgar & Connor 2000).

Descriptions and measurements given here follow the conventions of Connor & Edgar (1979) and are based primarily on plants of North American and Hawaiian origin. Meiotic chromosome counts of *R. racemosum* and *R. richardsonii* were determined on plants grown from seed obtained from collections originating in California. These counts are indicated in square brackets after the original collection citation. Voucher specimens for chromosome counts of *R. racemosum* and *R. richardsonii* are deposited at DAO with associated material at DAO, CHR and UC. Counts of plants of New Zealand provenance are presented for *R. caespitosum*; vouchers are deposited at AK and CHR. Illustrations of lemmas are prepared from North American (line drawings) and New Zealand (color paintings) material.

This study is primarily focused on species that have become naturalized in the United States; however, a number of specimens of cultivated material are included since undetected escape may well have occurred. Specimens from cultivation were included to improve the species' descriptions, when it was felt that they provide examples of poorly known species, or when they provide information on introduction sites.

#### TAXONOMIC TREATMENT

**Rytidosperma** Steud., Syn. Pl. Glum. 1:425. 1854. TYPE: *Rytidosperma lechleri* Steud.

*Notodanthonia* Zotov, New Zealand J. Bot. 1:104. 1963. TYPE: *Notodanthonia unarede* (Raoul) Zotov.

*Austrodanthonia* H.P. Linder, Telopea 7:269. 1997. TYPE: *Austrodanthonia caespitosa* (Gaudich.) H.P. Linder.

**Plants** perennial, densely or loosely cespitose, sometimes shortly rhizomatous. **Culms** (1.5–)30–90(–140) cm, erect or nodding. **Leaves** usually mostly basal; **sheaths** open almost to the base, glabrous or hairy, apices usually with tufts of hairs, sometimes extending across the collar; **ligules** a rim of hairs; **blades** persistent or disarticulating, flat, involute or convolute, glabrous or variously pubescent. **Inflorescences** terminal, racemes or panicles. **Spikelets** somewhat laterally compressed, with 3–10 florets; **florets** bisexual, chasmogamous or cleistogamous, terminal florets reduced; **disarticulation** above the glumes and between the florets; **glumes** (2–)8–20 mm long, subequal or equal, usually exceeding the florets (excluding awns), stiffly membranous, 3–13 veins, usually with scarious margins; **calluses** sharp or somewhat blunt with lateral tufts of stiff hairs, disarticulation oblique; **lemmas** (the main lemma body) ovate to lanceolate, with 2 complete or incomplete transverse rows of tufts of stiff hairs, sometimes reduced to marginal tufts, 5–9(–11) veins, apices bilobed, the **lobes** usually at least as long as the body, acute or acuminate with a long awn-like arista; a central **awn** between the lobes and longer than them, usually proximally twisted below into a column, usually geniculate or reflexed; **lodicules** 2, fleshy, usually with apical hairs or glabrous; **anthers** vary greatly in size depending on whether they are from cleistogamic or chasmogamic flowers (usually < 1.2 mm and > 1.8 mm, respectively). **Caryopses** 1.2–3 mm long, obovate to elliptic, golden to dark brown, free; **hila** punctiform to somewhat elliptic. **Cleistogenes** not formed.  $x_2 = 12$  (Murray et al. 2005). Name from the Greek *rhytidōs*, "wrinkles," and *sperma*, "seed" (vide Connor & Edgar 1979).

KEY TO THE SPECIES OF *RYTIDOSPERMA* NATURALIZED IN THE UNITED STATES OF AMERICA

1. Upper lemma hairs in isolated tufts or at margins only and not forming a continuous transverse row, lower tufts in a continuous row.
  2. Callus of second lemma 0.5–1.5 mm long, its hairs usually overlapping the lower row of lemma hairs; lateral lemma lobes 5–13 mm long, gradually narrowed to a fine awn-like arista \_\_\_\_\_ **R. penicillatum**
  2. Callus of second lemma 1–1.5 mm long, its hairs rarely or just reaching lower row of lemma hairs; lateral lemma lobes 5–10 mm long, abruptly narrowed to a fine awn-like arista \_\_\_\_\_ **R. racemosum**
1. Lemma hairs in two continuous transverse rows of tufts, with or without hairs between the rows.
  3. Central awn 10–20 mm long, column 4–5 mm long \_\_\_\_\_ **R. caespitosum**
  3. Central awn usually less than 10 mm long, column 0.5–3 mm long.
    4. Lemmas 1.8–2.4 mm long; awn column 2.5–3 mm long, distinctly twisted; lower row of lemma hairs usually not reaching upper row \_\_\_\_\_ **R. biannulare**
    4. Lemmas 3–4 mm long; awn column 0.5–1 mm long, sparingly twisted; lower row of lemma hairs overlapping upper row \_\_\_\_\_ **R. richardsonii**

***Rytidosperma biannulare*** (Zotov) Connor & Edgar, New Zealand J. Bot. 17:324. 1979. (**Fig. 1C, 3B**). *Notodanthonia biannularis* Zotov, New Zealand J. Bot. 1:116. 1963. *Austrodanthonia biannularis* (Zotov) H.P. Linder, Telopea 7:270. 1997. TYPE: NEW ZEALAND. Northland, Waitangi Forest, roadside, abundant, 28 Nov 1953, V.D. Zotov (HOLOTYPE: CHR 85021).

*Danthonia semiannularis* auct. amer., non (Labill.) R. Br.

**Plants** caespitose. **Culms** 30–85 cm, erect, smooth and glabrous, glabrous below inflorescence, branching intravaginal. **Leaves** mostly basal, exceeded by the culms, flag leaf blades usually reaching or exceeding the inflorescences; **sheaths** mostly glabrous, often purplish distally, apical tufts of hairs to 5 mm or sometimes absent; **ligules** 0.3–0.5(–1) mm; **blades** 30–40 cm long, to 5 mm wide, usually involute, margins, apices, and sometimes adaxial surfaces scabrous, young blades sparsely pilose, becoming glabrous at maturity. **Inflorescences** paniculate, 10–20 cm long, narrow and compact; **rachis** scabrous; **pedicels** shorter than spikelets, scabrous. **Spikelets** (7–)10–15 mm long, with 6–7 florets; **glumes** 7.5–11(–13.2) mm long, surpassing florets, subequal, lanceolate, acute, glabrous, light green to stramineous usually purple at margins and apex; **lower glumes** 5–7(–9) veins; **upper glumes** 5 veins; **rachilla segments** 0.3–0.5 mm long; **calluses** 0.5–0.7 mm long, hairs to about 1 mm and reaching the lower lemma hairs; **lemmas** 1.8–2.4(–2.8) mm long, hairs of lower row usually not or only just reaching the upper row, lower row sometimes ill-defined, hairs of upper rows reaching or surpassing the awn column apex but not the apex of the lemma lobes, with short scattered hairs (rarely glabrous) between the rows; **lobes** 3.5–5(–8.5) mm long, acuminate; **awn** 6–10(–12.5) mm long, twisted column 2.5–3 mm long; **paleas** 2.5–4.6 mm long, exceeding the lemma sinuses, obovate, emarginate, sparsely hairy between the veins, margins usually with long hairs, veins ciliate; **anthers** 0.8–1.6 mm long. **Caryopses** 1.2–1.9 mm × 0.6–0.8 mm; **embryos** 0.5–0.8 mm long; **hila** 0.3–0.6 mm long.  $2n = 48$ ; New Zealand plants (Murray et al. 2005).

A single collection from southwestern Oregon (Peck 23954) and another from Maui (Hobdy 2389) provide the only evidence that this species may have naturalized in the United States, although cultivated specimens from Santa Cruz Co., California, have also been seen (Fig. 4A). The species has been grown experimentally in North America under the name *Danthonia semiannularis* (Labill.) R. Br., possibly as early as 1905 (Weintraub 1953). However, as pointed out by Vickery (1956), *D. semiannularis* is a name that “has been used for almost any but the true species” and more than one species was probably imported to North America under this name. Since tetraploid *R. biannulare* is regarded as native to New Zealand and unknown in Australia, this species may have been more recently introduced than the early 20th Century importation of Australian species.

Whitney et al. (1939) and Wagner et al. (1999), respectively, reported *R. semiannulare* as introduced to the state of Hawai‘i (on Molokai) in 1903 and first collected (on Maui) in 1937. The 1937 specimen (Hosaka 1767) is, however, referred to *R. caespitosum*. Label data on a relatively recent collection of *R. biannulare* from West Maui (Hobdy 2389) suggest that this species has naturalized there.

Specimens examined: **CALIFORNIA. Santa Cruz Co.:** Ives plots near Aptos, Corralitos area, [cultivated], 20 May 1940, P.B. Dickey 920,



FIG. 1. Lemmas of *Rytidosperma*. A. *R. penicillatum*. B. *R. racemosum*. C. *R. biannulare*.

D920 (AHUC, US). **HAWAII. Maui:** West Maui, Hanaulaiki, elev. 3500 ft, May 1985, R. Hobdy 2389 (BISH). **OREGON. Curry Co.:** 5 mi S of Gold Beach, shady bank, 23 Jul 1945, M.E. Peck 23954 (WILLU).

***Rytidosperma caespitosum*** (Gaudich.) Connor & Edgar, New Zealand J. Bot. 17:325. 1979. (**Fig. 2B, 2C, 3C**). *Danthonia caespitosa* Gaudich. in Freycinet, Voy. Uranie Bot. 408. 1829. *Notodanthonia caespitosa* (Gaudich.) Zotov, New Zealand J. Bot. 1:117. 1963. *Austrodanthonia caespitosa* (Gaudich.) H.P. Linder, Telopia 7:271. 1997. TYPE: AUSTRALIA. WESTERN AUSTRALIA: Nouveau Hollande, Baie des C[hiens]-Marins [Shark's Bay], C. Gaudichaud-Beaupré (HOLOTYPE: P; ISOTYPE: K, BM).

*Danthonia varia* Nees, London J. Bot. 2:416. 1843. *Danthonia semiannularis* var. *varia* (Nees) Domin, Biblioth. Bot. 20(85):363. 1915. TYPE: AUSTRALIA. WESTERN AUSTRALIA: Swan River, 1839, J. Drummond 161. (LECTOTYPE: CGE; ISOLECTOTYPE: BM, K, NSW).

**Plants** densely to loosely caespitose, sometimes shortly rhizomatous. **Culms** 43–80 cm, erect, smooth and glabrous, glabrous or sparsely scabrous immediately below the inflorescence, branching intravaginal (or rarely extravaginal). **Leaves** mostly basal, usually exceeded by culms, flag leaves sometimes reaching inflorescence; **sheaths** glabrous or pilose, apical tufts of hairs 1–4 mm long, sometimes scanty; **ligules** (0.3–)0.5–1.2 mm long; **blades** 6–25 cm long, 1.5–3 mm wide, involute or more or less flat, glabrous or variously pubescent. **Inflorescence** paniculate, 5–11 cm long, linear to ovate, more or less compact; **rachis** scabrous to somewhat pubescent; **pedicels** shorter than spikelets, scabrous to somewhat pubescent. **Spikelets** 10–20 mm long, 4–9 florets; **glumes** 9–18(–20) mm long, surpassing florets, subequal to unequal, lanceolate, acuminate, glabrous or sometimes with scattered long hairs, light green to stramineous often purple at margins and apex; **lower glumes** (1–)3–5(–7) veins; **upper glumes** (3–)5–7(–9) veins; **rachilla segments** 0.1–0.4 mm long; **calluses** 0.4–1.5 mm long, hairs to about 1.5 mm long and usually reaching lower lemma hairs; **lemmas** 2.3–4 mm long, hairs of lower row to about 1.5 mm long and reaching the upper row, hairs of upper row to about 3.5 mm long and reaching or surpassing the palea apex but not apex of awn column or lemma lobes, glabrous between the rows; **lobes** (6–)7–10 mm long, acuminate or aristate; **awn** 10–20 mm long, tightly twisted column 4–6 mm long; **paleas** 2.5–5.5 mm long, surpassing lemma sinus, lanceolate to obovate, emarginate, glabrous between the veins, margins with a few long hairs, veins ciliate; **anthers** 0.5–2.6 mm long. **Caryopses** 1.7–2.3 mm × 0.8–1.1; **embryos** 0.7–1 mm long; **hila** 0.25–0.7 mm long.  $2n = 24, 48, 72$ ; Australian plants (Abele 1959; Brock & Brown 1961; Waters et al. 2010).  $2n = 24$ ; New Zealand plants (B.G. Murray & J.P. de Lange, hic comm.; AK 25913C, CHR 549710).

Grasslands, pastures, rangelands and disturbed areas up to 200 m. A highly variable and widespread species with co-occurring polyploid races indigenous to southern Australia (Vickery 1956; Abele 1959; Brock & Brown 1961; Waters et al. 2010). *Rytidosperma caespitosum* has naturalized at a few scattered locations in California (Berkeley, Pescadero and San Diego regions), and has been cultivated at Pullman, WA, and several sites in California (Fig. 4B). Two collections from Hawai'i by Hosaka in the 1930s are referred to this species, but the lack of recent collections suggests that it may not have persisted. It has also been naturalized in New Zealand since at least 1892 (Zotov 1963). It is listed, with some uncertainty, among the species introduced to the United Kingdom through discarded wool-waste (Lousley 1961; Ryves 1988).

Specimens examined: **CALIFORNIA. Alameda Co.:** Berkeley, grass garden, [cultivated], T.O. 600, SPI 54736, 24 May 1926, J.A. Denny s.n. (AHUC); Berkeley, Oxford Tract, [cultivated], 15 Jun 1929, B.P. Kennedy s.n. (AHUC); Pleasanton, [cultivated], origin: Australia, New South Wales, P.I. 238-283, T.O. 2512 raised at the SCS Plant Materials Center (No. PL 58-58), 19 Oct 1959, B. Crampton s.n. (AHUC); mouth of Strawberry Canyon in Oakland/Berkeley hills, east side of UC campus, southwest slope overlooking stadium ("Tightwad Hill"), southwest facing slope, grassland just below eucalyptus grove and above pines, 16 Feb 2002, B. Ertter 17815 [p.p.] (DAO, UC); Berkeley, NW edge of Strawberry Canyon on E edge of main UC campus, NE of main "viewing area" for "Tightwad Hill" overlooking football stadium, E side of eucalyptus grove, 26 Jun 2003, B. Ertter 18231a (CHR, DAO, UC). **Butte Co.:** Chico, [cultivated], S.P.I. No. 17205, seed from Richmond, New S. Wales, H.W. Potts 1-20-06, 7 Sep 1910, C.V. Piper s.n. (US). **San Diego Co.:** Lusardi Creek MSCP parcel: ridges S of Lusardi Creek, 0.6 km NNE Low South Survey Marker, T13S, R3W, SW/4 SW/4 sect. 26, rocky ridge on cobbly clay in openings of chamise chaparral, with *Adenostemma fasciculatum*, *Lotus scoparius*, *Mimulus puniceus* and *Mirabilis californica*, alt. 93 m, UTM 11S 0484470 m E 3651910 m N, clumped perennial, culms to 0.4 m tall, locally common, 18 Apr 2001, F.M. Roberts 5434 (RSA); near Fairbanks Ranch, ridge S of Lusardi Creek, ca. 0.2 km north San Dieguito Rd. and 1.3 km NE Fairbanks Lake, Rancho Santa Fe Z11S 0484468 mE, 3651734 mN, southeast-facing slope on clay soil in mixed grassland bordering coastal sage scrub, associated with *Stipa pulchra*, *Avena barbata*, *Vulpia myuros*, *Erodium cicutarium* and *Artemisia californica*, bordering fresh grading, alt. 83 m/ft [sic], 29 Mar 2005, F.M. Roberts 6136 (UCR). **San Mateo Co.:** Santa Cruz Mountains, Cascade Ranch State Park, between Whitehorse Creek and Cascade Creek, 4 Aug 1992, G. Clifton s.n. (UC). **Yolo Co.:** Agronomy Experimental Areas, Davis Campus, T.O. 2512, Row E-40, [cultivated], origin: Australia, New



FIG. 2. Lemmas of *Rytidosperma*. A. *R. richardsonii*. B. *R. caespitosum* (Berkeley). C. *R. caespitosum* (San Diego).



FIG. 3. Lemmas of *Rytidosperma*. A. *R. penicillatum*. B. *R. biannulare*. C. *R. caespitosum*.

South Wales, P.I. 238-283 thru SCS Plant Materials Center, Pleasanton (PL 58-58) 1959, 7 May 1962, B. Crampton s.n. (AHUC). **HAWAII.** **Maui:** Haleakalā, Puu Nianiau, common in open pasture, alt. 6000 ft, 28 Jan 1937, E.Y. Hosaka 1767 (BISH); Haleakalā, Makawao, common in grassy slope among *Styphelia*, elev. 5000 ft, 12 Apr 1939, E.Y. Hosaka 2472 (BISH). **WASHINGTON. Whitman Co.:** Pullman, [cultivated], S.P.I. No. 17203, seed from Richmond, New S. Wales, H.W. Potts 1-20-06, 1907, C.V. Piper s.n. (US).

**Rytidosperma penicillatum** (Labill.) Connor & Edgar, New Zealand J. Bot. 17:327. 1979. (Fig. 1A, 3A).

*Arundo penicillata* Labill., Nov. Holl. Pl. Spec. 1:26, t. 34. 1805. *Danthonia penicillata* (Labill.) P. Beauv., Ess. Agrostogr. 153, 160. 1812.

*Danthonia racemosa* var. *penicillata* (Labill.) Benth., Fl. Austral. 7:594. 1878. *Notodanthonia penicillata* (Labill.) Zotov, New Zealand J.

Bot. 1:122. 1963. *Austrodanthonia penicillata* (Labill.) H.P. Linder, Telopia 7:272. 1997. TYPE: AUSTRALIA. TASMANIA: Habitat in capite

Van Diemen, *Labillardière* (HOLOTYPE: FI-W; photo K).

*Danthonia pilosa* auct. amer., non R. Br.

**Plants** densely to loosely caespitose to somewhat spreading, shortly rhizomatous. **Culms** (22–)30–90 cm, erect, usually smooth and glabrous, usually scabrous-pubescent immediately below the inflorescence, branching extravaginal, cataphylls scaly. **Leaves** mostly basal and greatly exceeded by the culms, flag leaf blades usually not reaching the inflorescence; **sheaths** densely hairy or glabrous, apical tufts of hairs 1–3.5 mm long; **ligules** (0.1)0.3–1 mm long; **blades** to 30 cm long and to 5 mm wide, flat, folded, or involute, glabrous, scabrous or pubescent. **Inflorescences** racemose or paniculate, (3–)4–10 cm long, ovate to linear, compact; **rachis** scabrous to finely pubescent; **pedicels** shorter than the spikelets, glabrous, scabrous or finely pubescent. **Spikelets** 9–15(–18) mm long, 5–7(–10) florets; **glumes** (7.5–)8–13(–17.5) mm long, surpassing florets, subequal, lanceolate, glabrous, scabrous, or sometimes with scattered hairs, light green to stramineous often purple at margins and apex; **lower glumes** 5–9(–11) veins; **upper glumes** 5–7(–9) veins; **rachilla segments** 0.2–0.5 mm long; **calluses** 0.5–1.3 mm long, hairs about 1.5 mm long and usually reaching the lower lemma hairs; **lemmas** (2–)2.5–4.2 mm long, 9(–11) veins, lower row of hairs continuous or with weak (rarely absent) central tufts, hairs of the marginal tufts usually reaching the upper row of hairs, upper row of hairs composed of 2 marginal tufts, sometimes with 2 additional scanty tufts between, hairs reaching or slightly exceeding the base of the awn, otherwise glabrous; **lobes** 5–11(–13) mm long, acuminate, aristate; **awn** (7–)9–17.5 mm long, tightly twisted column 1.5–4 mm long, somewhat reflexed at base and revealing palea apex or not; **paleas** 3–6 mm long, exceeding the lemma sinuses, emarginate, intercostal region glabrous or scabrous, margins glabrous or with sparse long hairs, veins ciliate; **anthers** 0.4–2.7 mm long. **Caryopses** 1.8–2.5(–3) mm × 0.8–1.1(–1.6) mm; **embryos** 0.7–1(–1.5) mm long; **hila** (0.3–)0.4–0.5(–0.7) mm long.  $2n = 24$ ; Australian plants (Abele 1959; Brock & Brown 1961) and Californian plants (Myers 1947 [as *Danthonia pilosa*]).

Commonly growing on dry, nutrient-poor soils. Habitats include pastures, rangelands and disturbed areas at elevations up to about 800 m in California, and about 1675–2840 m in Hawai'i. It is a common weed in coastal regions of California and southwestern Oregon (Fig. 4C). At best, only of moderate forage value in the United States where it is usually considered a troublesome pest competing with more desirable species (Murphy & Love 1950; Stone et al. 1992).

An Australian species, *R. penicillata* has been incorrectly known in the United States for many years under the name *Danthonia pilosa* R. Br. (e.g., Hitchcock 1951; Sampson et al. 1951; Weintraub 1953). Various common names have been used, including hairy danthonia, hairy oatgrass, Australian oatgrass and poverty grass. Although it is considered a poor quality forage grass, it was introduced and tested in the continental states in 1911 and again in 1921 (Weintraub 1953). By the 1940s it had become a troublesome weed at scattered localities mainly in coastal areas from southwestern Oregon to central California (Murphy & Love 1950; Sampson et al. 1951). Introduced to the Hawaiian Islands about 1910 (Whitney et al. 1939; BISH 624327) and to New Zealand as early as 1840 (Zotov 1963), it is now well established in these regions. In the United Kingdom, it has been reported as introduced with wool-waste (Lousley 1961; Ryves 1988), but has not become fully naturalized (Stace 1997).

Specimens examined: **CALIFORNIA. Alameda Co.:** Berkeley, [cultivated], experimental plot planted 1914, seed from Brunning Co., Australia, 16 Jul 1916, P.B. Kennedy s.n. (AHUC); Berkeley, campus, [cultivated], seed collected at Davis, Calif., 9 Jul 1920, P.B. Kennedy 3073 (AHUC, DAO), 3389 (AHUC, DAO); Berkeley, Cragmont Park, from lawn where growing as weed, an aggressive weed, hard to



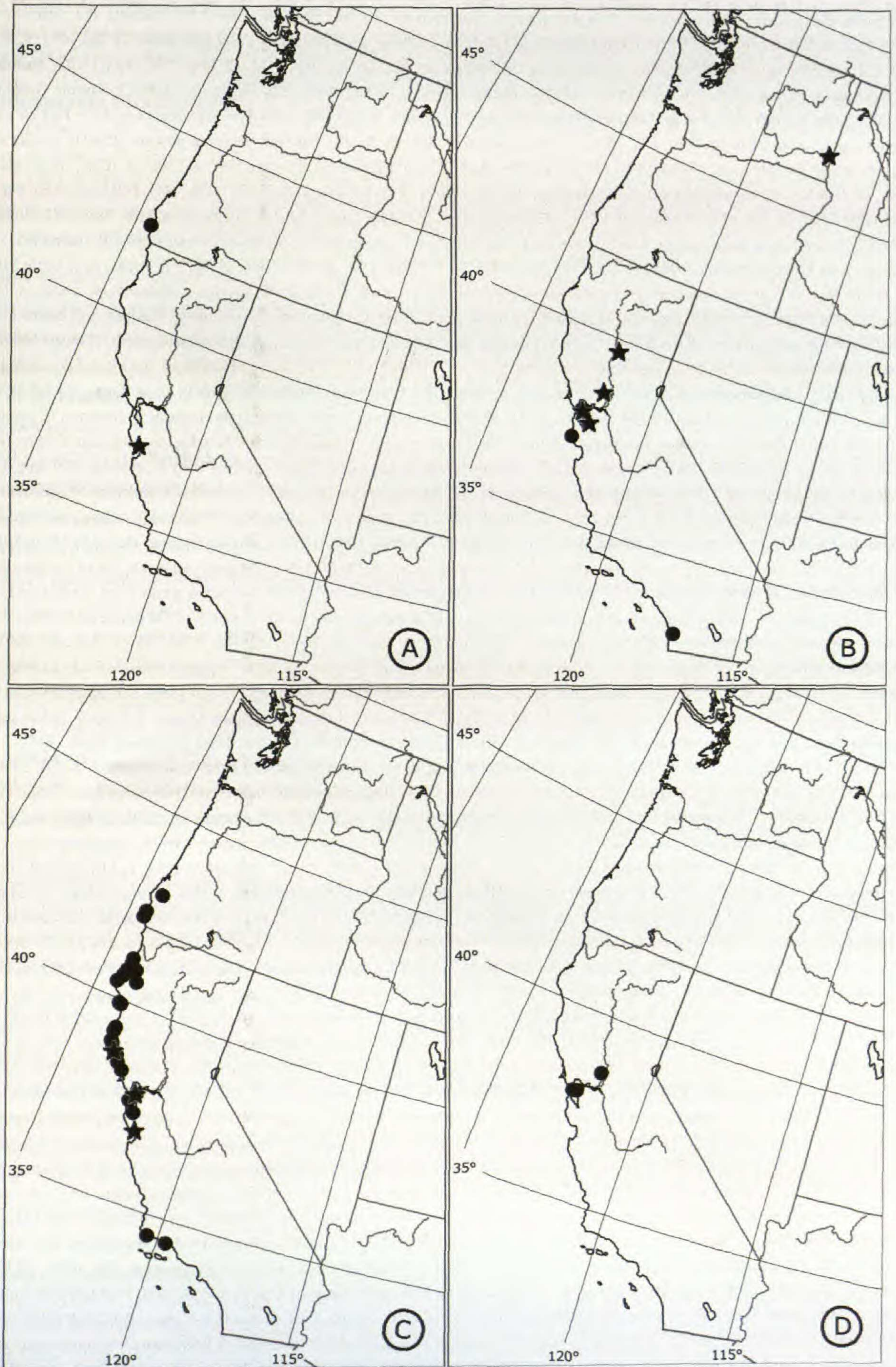


FIG. 4. Distribution of *Rytidosperma* species in western North America; circles indicate naturalized plants, stars indicate cultivated plants. A. *R. biannulare*. B. *R. caespitosum*. C. *R. penicillatum*. D. *R. racemosum*.

control particularly where lawn is watered little, horticulture specimen no. 20, Jun 1950,  $2n = 24$  (J.M.J. DeWet), G.L. Stebbins 3202 (AHUC, UC); Berkeley, campus of Univ. of California, N of Life Sciences Bldg., growing under *Eucalyptus* trees, 11 Sep 1952, R.W. Pohl 7201 (CAS); north Berkeley, weedy sites in residential area, including as weed in lawns, 19 Jul 2000, B. Ertter 17419 [p.p.] (UC). **Humboldt Co.:** Loleta, coast, 6 Aug 1938, B.A. Madson s.n. (AHUC); Ureka [Eureka], 15 Aug 1940, H.B. Shontz s.n. (AHUC); Bayside Golf Links, elev. 100 ft, probably introduced in grass seed mixture, forming a close turf, 16 Jun 1941, Mrs. Wm. Grotzman s.n. (UC); Patrick's Point State Park, open meadow, 28 Jul 1941, F.W. Peirson 13113 (RSA); at Hungry Hollow on Bald Mt., in sheep pasture, 2500 ft, locally abundant as if a recent introduction, 17 Aug 1941, J.P. Tracy 16994 (AHUC, UC); Bald Mountain, Mar 1942, J. Tracy s.n. (CAS); near "Hungry Hollow" on Bald Mt., locally abundant in sheep pasture, 2000 ft, 28 Jun 1942, J.P. Tracy 17267 (DS, HSC, MO, POM, UC, US); Parrott's Ranch, Table Bluff, ca. 1.5 mi N of Loleta, Jun 1947, A.H. Murphy s.n. (AHUC); Loleta, Patrick's Point State Park, July 1947, R. Tofsrud 200 (AHUC); near Angels Ranch on the Bald Mt., road at Hungry Hollow, in sheep pasture, 2500 ft, 11 Aug 1949, J.P. Tracy 18451 (UC); Bear River, 3 mi E of Capetown, 19 Jul 1956, R. Evans s.n. (AHUC); T 3 N, R 1 W, Sec. 16, about 20 mi S of Arcata near Little Salmon Creek on the Marvin Stapp Ranch, open grassy pasture below the house, elev. ca. 150 ft, assoc. species: *Anthoxanthum aristatum*, *Holcus lanatus*, *Prunella vulgaris* and *Rubus procerus*, 24 Jun 1967, T. Hoyle 261A-67 (HSC); Humboldt State College Campus, just below Founder's Hall, near the steps to the Science Bldg., T 6 N, R 1 E, Sec. 28, cultivated lawn, assoc. species *Holcus lanatus*, *Plantago lanceolata*, *Trifolium repens* and other cultivated grasses, elev. ca. 100 ft, 5 Jul 1967, T. Hoyle 274-67 (HSC); Trinidad Head, large coastal rock outcrop, Smith 12151 (HSC). **Mendocino Co.:** near Pt. Arena, open woods, 7 Jul 1938, W.A. Silveus 2935 (DAO); Point Arena, 15 Jul 1941, D. Jensen s.n. (DAV); Point Arena, August 1949, W.H. Brooks 111 (AHUC); ½ mi N of Albion, along State Highway 1, common in patches in grazed coastal mesa flats, surrounding area boggy, 26 Jul 1955, B. Crampton 3041 (AHUC); city of Mendocino, common in open coastal mesa above sea, 27 Jul 1955, B. Crampton 3128 (AHUC); on Orr Spring Road, 1.7 mi E of California Hwy. 1, elev. ca. 550 feet, 25 Jun 1964, R.E. Frenkel 625 (CAS); 4.5 mi S of Mendocino, State Hwy. 1, 29 Jun 1966, B. Crampton 7792 (AHUC); Sinkyone Wilderness State Park, T23N R18W SW ¼ Sec. 22, Hales Grove, 7.5" USGA quad, about 10 mi due W of Leggett and 60 mi N of Fort Bragg, mouth of Usal Creek on the Pacific Ocean, flood plain, coastal prairie, disturbed by livestock grazing and upstream logging, elev. 0 ft, 19 Jul 1988, F. Bowcutt 1146 (HSC); Sinkyone Wilderness State Park, T24N R19W SE ¼ Sec. 9, Bear Harbor 7.5 Quad., 15 air mi SW of Garberville, 60 air mi SSE of Eureka, ¼ mi SE Jone Beach, 1.25 mi SW Four Corners, coastal grassland of marine terrace, grazed and used as dairy farm prior to State acquisition with periodic prescribed burns, W aspect 10 slope, elev. 140 ft, 50.75 yds W of old homesite at Jones Ranch, associated with *Holcus lanatus*, *Linum*, *Plantago lanceolata*, *Erechtites*, *Senecio jacobaea*, *Rubus vitifolius*, 7 Jul 1989, F. Bowcutt 1366 (DAV, HSC). **Santa Barbara Co.:** Santa Barbara Coastal Plain region, coastal plains & basins, in lawn of upper Hillside Park, 13 May 1947, C.F. Smith 2009 (AHUC, CAS, RSA, US); Santa Ynez Mts, Hillside Park [upper], Santa Barbara, 22 Jul 1949, C.F. Smith 2406 (AHUC, SBBG); Santa Ynez Mts, San Augustin Cyn, Cuesta Rd on Hollister Ranch, ca. N of San Augustin Arroyo, C.F. Smith 12686 (SBBG). **Santa Clara Co.:** Palo Alto, University Ave. at Chaucer St., uncultivated in parking area, 29 Jun 1960, J.T. Howell 35482 (AHUC, CAS, DAV, DS); Palo Alto, Chaucer St. and University Ave., in weedy parking lot between sidewalk and street at intersection, 30 Jun 1960, J.H. Thomas 8808 [DS, RSA]; Palo Alto, wasteland, J.T. Howell s.n. (AHUC, JEPS). **Santa Cruz Co.:** near Aptos, Ives plots, [cultivated], 20 May 1940, P.B. Dickey D921 (US). **Sonoma Co.:** Gualala, experimental plots, [cultivated], 1915, P.B. Kennedy s.n. (AHUC); Miller Ridge, open grassland in redwood belt with *Bromus mollis* etc., 2 Jul 1957, J.C. Roos 6651 (CAS, RSA, UCR); Stewart's Point, along State Hwy 1, 2 mi N, slopes above sea, below bishop pine forest, 22 Jul 1957, B. Crampton 4358 (AHUC, UC); along State Hwy. 1, 11.7 mi S of Stewart's Point, slopes above the sea, 22 Jul 1957, B. Crampton 4392 (AHUC); Sea Ranch, near State Highway 1, Unit 1 Owner's Map, tufted perennial, 50 feet back from ocean bluffs, 24 Jun 1974, M.M. Hektner & C. Hendel 068 (DAV); 3.1 mi N of Fort Ross Road, on Seaview Road, elev. 1300 ft, 23 Jun 1964, R.E. Frenkel 623 (CAS); Annapolis Road area just below and W of landing strip at the Sea Ranch, disturbed sites in annual grassland, elev. ca. 300 ft, 30 Nov 1980, R.D. Stone 332 (JEPS); The Sea Ranch, 2 Aug 1981, M.P. Wells s.n. (CAS); The Sea Ranch, Timber Preserve of Oceanic of California Inc., 3 Aug 1983, M.P. Wells s.n. (CAS); Bodega Bay, behind community center on W side of Hwy 1 N of town, coastal meadow, locally abundant, in patches, with *Briza maxima*, 19 Jul 2003, B. Ertter 18246 (CHR, DAO, UC). **Yolo Co.:** Davis, grass garden, [cultivated], 13 Jun 1919, Leonard 3073 (AHUC). **HAWAII. Hawaii:** Mauna Kea, Pohakalua [Pohakuloa] Military Camp, site B-2, T-1, #5, 1979 burn area, elev. 8000 ft, K. Adee s.n. (BISH); North Hilo, Humuula, near Puu Oo, fairly wet pasture, elev. 7000 ft, 2 May 1932, G.R. Ewart III 250 (BISH); slope above Humuula, 7000–7500 ft, 30 Jul 1935, E.H. Bryan, Jr. s.n. (BISH); Kahohe, Mauna Kea, Hamakua, occasional in dry open pasture, elev. 6500 ft, 12 Sep 1936, E.Y. Hosaka 1596 (BISH); North Hilo, Humuula Sheep Sta., elev. 6700 ft, 13 Jun 1938, E.Y. Hosaka 2316 (BISH); near Pohakuloa, Puu Omaoiki, elev. 7000 ft, 3 Apr 1962, E. Kosaka [sic] 12 (BISH); on road from saddle (Humuula Sta.) to State Park cabins (Halepohaku), S slope of Mauna Kea volcano, tussock grassland (*Deschampsia nubiginea*, *Trisetum glomeratum*, *Danthonia* sp., many spp. intro.) *Sophora chrysophylla* savanna, on porous basaltic sands and volcanic ash slopes, elev. 8200–9200 ft, 23 Jun 1967, H.H. Iltis & C.M. Iltis H-190 (RSA), H-190a (BISH); Puu Laau, weed growing near the hunter's cabin, elev. 7450 ft, 18 Jan 1975, D. Herbst 5224 (BISH); saddle area along road to Mauna Loa observatory, ½ mi from Pu'u Huluhulu, growing with *Juncus*, *Tetramolopium*, *Vaccinium* and grasses near native scrub vegetation, elev. 6500–7000 ft, 15 Jun 1981, J. Davis 523 (BISH); N slope of Mauna Kea, Makai of Puu Kole near Hanapoe Gulch, 19°53'25"N, 155°27'18"W, subalpine shrubland with cinder substrate, associated vegetation Pukiawe, mamane, 23 Jul 2004, F. Starr & K. Starr 040723-9 (BISH). **Maui:** Haleakalā nursery, volunteer, 13 Sep 1938 (BISH); west rim of Haleakalā Crater, alpine grassland at Kalahaku Overlook, weeds and occasional native grasses along road, foot path and *Argyroxiphium sandwicense* (SILVERSWORD) enclosure, alpine grassland, elev. 9320 ft, 7 Aug 1967, H.H. Iltis & C.M. Iltis H-543 (RSA); Haleakalā Crater, base of Crystal cave, on open cinder slope with *Deschampsia*, *Styphelia*, *Sophora*, elev. 2195 m, 25 Jun 1998, B. Haus s.n. (BISH); on side of Crater Rd., 20°45'N, 156°16'W, pastures, *Pennisetum clandestinum*, elev. 5500 ft, 13 Sep 2000, F. Starr & K. Martz 000913-3 (BISH); Makawao Dist., Kamaole, Kula Forest Reserve, alongside the Haleakalā Ridge

Trail, 20°40'N, 156°20'W, alien forestry plantings, elev. 6300 ft, 15 Jul 2002, H.L. Oppenheimer et al. H70208 (BISH). **OREGON. Curry Co.:** 5 mi S of Gold Beach, grassy slope, 23 Jul 1945, M.E. Peck 23955 (WILLU); Pistol River State Park, on coastal dunes, with *Phacelia argentea*, 28 Jul 1982, J. Kagan 728822 (OSC). **Coos Co.:** Gaylord, growing in a hill pasture, 22 Aug 1956, J.R. Thienes s.n. (OSC).

***Rytidosperma racemosum*** (R. Br.) Connor & Edgar, New Zealand J. Bot. 17:327. 1979. (**Fig. 1B**). *Danthonia racemosa* R. Br., Prodr. 177. 1810. *Danthonia penicillata* var. *racemosa* (R. Br.) Rodway, Tasmanian Flora 267. 1903. *Notodanthonia racemosa* (R. Br.) Zotov, New Zealand J. Bot. 1:121. 1963. *Austrodanthonia racemosa* (R. Br.) H.P. Linder, Telopea 7:273. 1997. TYPE: AUSTRALIA. NEW SOUTH WALES: Port Jackson, 1802–1805, R. Brown 6235. (HOLOTYPE: BM; ISOTYPE: K; fragments: CHR, MEL, PERTH).

*Danthonia pilosa* var. *racemosa* Buchan., Indig. Grasses New Zealand t. 33(2) B. 1879. TYPE: NEW ZEALAND: [probably] Wellington, summer 1878–1879, J. Buchanan (HOLOTYPE: WELT 59580).

**Plants** densely to loosely caespitose, shortly rhizomatous. **Culms** 20–60(–90) cm, erect, smooth and glabrous, usually scabrous immediately below the inflorescence, branching extravaginal, cataphylls scaly. **Leaves** mostly basal, exceeded by or as long as the culms, flag leaf blades usually reaching the inflorescences; **sheaths** glabrous or with scattered hairs, with apical tufts of hairs, hairs to 4 mm long; **ligules** 0.2–0.5 mm long; **blades** (5–)15–25(–75) cm long, to 2 mm wide, flat or involute, glabrous or pubescent. **Inflorescences** racemose or with a few branches, 5–15 cm long, lanceolate; **rachis** scabrous; **pedicels** shorter than spikelets, scabrous. **Spikelets** (7–)10–13(–16) mm long, 6–7(–10) florets; **glumes** (7–)8–13(–16) mm long, surpassing florets, subequal, lanceolate, subacute, glabrous or sometimes with a few hairs, light green to stramineous often purple at margins and apex; **lower glumes** (5–)7-veined; **upper glumes** 5(–7)-veined; **rachilla segments** 0.1–0.2 mm long; **calluses** (0.6–)0.9–1.5(–2) mm long, hairs 1.0–1.5 mm long and not or barely reaching the lower lemma hairs; **lemmas** 2.5–3.5(–4.5) mm long, (7–)9 veins, lower row of hairs dense, hairs not or just reaching the upper rows, upper row of hairs reaching or slightly exceeding the base of the awn, scanty medial tufts usually present or sometimes absent, glabrous elsewhere; **lobes** 5–10 mm long, abruptly aristate; **awn** 11–14 mm long, lightly twisted column 2–3 mm long, somewhat reflexed at the base and revealing palea apex; **paleas** 3.5–5 mm long, exceeding the lemma sinuses, emarginate, glabrous or with a few hairs, veins ciliate; **anthers** 0.3–2 mm long. **Caryopses** 1.7–2.1(–2.5) mm × 0.8–1.1(–1.3) mm; **embryos** 0.8–0.9 mm long; **hila** 0.4–0.5 mm long.  $2n = 24$ ; Australian plants (Abele 1959; Brock & Brown 1961) and Californian plants (this paper).

This highly variable species is endemic to southern Australia where it “displays a bewildering variety of forms” (Vickery 1956). Connor and Edgar (1979) described the upper hairs on the lemma as rarely forming a continuous row of tufts, but this state has not been observed in any material from North America. An extreme form with short abruptly acute or mucronate lemma lobes is often recognized as *R. racemosum* var. *obtusatum* (Benth.) Connor & Edgar, but all material from the United States is typical var. *racemosum*.

Naturalized primarily as a ruderal weed in disturbed areas less than 200 m in elevation. It is a common weed of lawns and roadsides around Berkeley, California (Blumler 2001; Ertter, personal observation), and has also been collected at Davis (Fig. 4D). St. John (1973) stated that it was introduced to Hawai‘i in 1937, but we were unable to locate specimens to confirm this.

Introduced and grown for forage trials at several locations in North America, this species is frequently confused with *R. penicillatum*. Although the earliest North America record located dates from cultivation at Berkeley in 1941, it was probably grown in earlier times under the name of *Danthonia pilosa*. It was present in New Zealand as early as 1840 (Zotov 1963). In the United Kingdom, var. *obtusatum* has been reported as introduced with wool-waste (Lousley 1961; Ryves 1988), but has not become fully naturalized (Stace 1997).

Specimens examined: **CALIFORNIA. Alameda Co.:** Berkeley, cultivated in the Agronomy Division grass garden, Row 15, plot 12, 1941, A.A. Beetle s.n. (AHUC, DAO); Berkeley, at corner of Hearst and Oxford, May 1951, A. Haig s.n. (AHUC, DAV); Berkeley, Campus of Univ. of California, Life Sciences Bldg., growing under *Eucalyptus* trees, 11 Sep 1952, R.W. Pohl 7201 (UC); Berkeley, UC Campus, along Hearst Ave sidewalk, Oxford Tract, volunteer, 25 Aug 1953, B. Crampton 1609 (AHUC); W side of Albany Hill, along path SE of condominiums, sandstone substrate, in open eucalyptus forest, very localized but common at this one locality, 13 Jun 1998, B. Ertter 16207 (DAO, UC); north Berkeley, weedy sites in residential area, including as weed in lawns, occasional, 19 Jul 2000, B. Ertter 17419 [p.p.] (DAO, UC); Mendocino Ave. at Marin Circle in north Berkeley, well-developed population in lawns of several adjacent residential lots, 19 Jun 2003, B.

*Ertter 18216* (CHR, DAO, UC); 859 Alameda N of Solano Ave. in north Berkeley, local population in lawns of adjacent residential lots, 19 Jun 2003, B. *Ertter 18217* (DAO, UC); Berkeley, 1601 Spruce St. just S of Cedar St., N of UC campus, local population at edge of sidewalk in single residential lot, 19 Jun 2003, B. *Ertter 18218* (CHR, DAO, UC); N of UC campus in Berkeley, 1770 Arch St. N of Hearst Ave., local population in streetside strip of single residential lot, 19 Jun 2003, B. *Ertter 18219* (DAO, UC); 1108 Fresno Ave. S of Monterey Ave. in north Berkeley, local population at edge of lawn and sidewalk of residential lot, 20 Jun 2003, B. *Ertter 18220* (CHR, DAO, UC); Berkeley NW of UC campus, 1766 Walnut St., local population at edge of lawn and sidewalk of residential lot, 20 Jun 2003, B. *Ertter 18221* (CHR, DAO, UC); north Berkeley, 11601 Bonita Ave. at Cedar St., local population at edge of lawn and sidewalk of single residential lot, 20 Jun 2003, B. *Ertter 18222* (CHR, DAO, UC); north Berkeley, NE corner of Hopkins St. and The Alameda, lush plants of population appearing at edges of lawns and sidewalks for several residential blocks, 20 Jun 2003, B. *Ertter 18223* (CHR, DAO, UC); Albany, W side of Albany Adult School on San Gabriel Ave. S of Brighton Ave., abundant and lush plants among neglected shrubbery along sidewalk, 21 Jun 2003, B. *Ertter 18224* (CHR, DAO, UC) [ $n = 12$ ]. **Marin Co.:** Angel Island, perimeter road just N of West Garrison, locally common as a roadside weed, 1978, G.H. True 8468 (AHUC). **Yolo Co.:** Davis, yard of B.A. Madson, 11 Jun 1951, B.A. Madson s.n. (AHUC).

***Rytidosperma richardsonii*** (Cashmore) Connor & Edgar, New Zealand J. Bot. 17:332. 1979. (**Fig. 2A**).

*Danthonia richardsonii* Cashmore, Commonw. Austral. C. S. I. R. Bull. 69: Appendix, 2. 1932. *Notodanthonia richardsonii* (Cashmore) Veldkamp, Taxon 29:297. 1980. *Austrodanthonia richardsonii* (Cashmore) H.P. Linder, Telopea 7:273. 1997. TYPE: AUSTRALIA. SOUTH AUSTRALIA: Werribee, 2 Dec 1932, A.B. Cashmore Ga63. (HOLOTYPE: AD (fide Vickery op. cit.: 281); ISOTYPE: BM, K, NSW).

**Plants** densely caespitose, without rhizomes. **Culms** 45–80(–100) cm, erect, smooth and glabrous, glabrous or sparsely scabrous immediately below inflorescence; branching intravaginal. **Leaves** mostly basal, exceeded by culms; flag leaf reaching inflorescence or not; **sheaths** glabrous, apical tufts of hairs 1–5 mm long sometimes scant; **ligules** 0.5–1.5 mm long; **blades** 10–50 cm long, 1.5–4 mm wide, flat or involute when dry, glabrous or sometimes adaxially scabrous. **Inflorescences** paniculate, 4–10 cm long, broadly lanceolate to ovate, compact; **rachis** glabrous to sparsely pubescent; **pedicels** shorter than spikelets, scabrous to pubescent. **Spikelets** 10–15 cm long, 4–6 florets; **glumes** 11–13 mm long, surpassing florets, subequal, broadly lanceolate to ovate, acute, glabrous, green to light green or stramineous with age, lacking purple pigments; **lower glumes** 7–11 veins; **upper glumes** 7–9 veins; **rachilla segments** 0.4 mm long; **calluses** 0.5–1 mm long, hairs 1–2.5 mm long, surpassing base of lower lemma hairs; **lemmas** 3–4.5 mm long, 2 continuous rows of hairs, the lower 1.5–4 mm long, surpassing the base of the upper row, the upper row 3.5–5 mm long, surpassing the lemma sinus, but not the apex of the lemma lobes, pubescent between the rows with shorter hairs; **lobes** to 4.5–6 mm long, aristate; **awn** 6.5–9 mm long, indistinct column 0.5–1 mm long with few twists; **paleas** 3.4–4.5 mm long, equaling or surpassing the lemma sinus, ovate, emarginate, pilose between the veins at the base and glabrous or somewhat pilose on the margins, veins ciliate; **anthers** 0.8 mm long. **Caryopses** about 2.5 × 1.5 mm; **embryos** about 1.5 mm long; **hila** about 0.5 mm long.  $2n = 48$ ; Australian plants (Abele 1959; Brock & Brown 1961) and Californian plants (Myers 1947; this paper).

Indigenous to southeastern Australia, *R. richardsonii* is known in an established population only at the University of California, Berkeley, campus. Here a small, but dense population grows in shrubby grassland at the edge of *Eucalyptus* groves, where it occurs with *R. caespitosum*.

Specimens examined: **CALIFORNIA: Alameda Co.:** Berkeley, NW edge of Strawberry Canyon on E edge of main UC campus, NE of main "viewing area" for "Tightwad Hill" overlooking football stadium, below eucalyptus grove, SE-facing grassland at edge of brush, locally well-established colony forming lush stand of perennial bunch-grass, scattered plants with a few flowering stems, 16 Feb 2002, B. *Ertter 17815* [p.p.] (DAO, UC); Berkeley, NW edge of Strawberry Canyon on E edge of main UC campus, NE of main "viewing area" for "Tightwad Hill" overlooking football stadium, E side of eucalyptus grove, ± dominant at this one site, in full sun (where all dried) to partial shade, 26 Jun 2003, B. *Ertter 18231* (CHR, DAO, UC) [ $n = 24$ ].

***Incertae sedis.***

**CALIFORNIA. San Mateo Co.:** San Bruno Mountains, Randolph Ravine, uncommon, in *Stipa pulchra* grassland, 17 Mar 1989, B. Johnson s.n. (CAS).

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Flahey prepared the line drawings of florets. The floret paintings by Keith R. West were originally prepared for the revision of New Zealand taxa by Connor & Edgar (1979), but were never published, except for that of *R. biannulare* which appeared in Edgar & Connor (2000). Two paintings are now published for the first time, about 30 years later. We thank CHR for permission to reproduce them here. Herbarium curators at AHUC, BISH, CAS, CDA, CHR, DAO, DAV, HSC, JEPS, MO, OSC, RSA, SBBG, UC, UCR, US, and WILLU are thanked for making material available for study.

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